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Management and Conservation Article

Short-Term Responses of Red Squirrels to Prescribed Burning in the Interior Pacific Northwest, USA

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ABSTRACT We quantified changes in density of red squirrels (*Tamiasciurus hudsonicus*) in response to prescribed fire in mixed coniferous forests of Idaho and Washington, USA, using a Before-After-Control-Impact design. We found no evidence that low-severity prescribed fires affected density of red squirrels; we estimated the change in red squirrel densities due to prescribed fire as −0.15 squirrels/ha (95% CI = −0.405–0.105). Squirrel density did, however, increase with increasing live tree density, shrub cover, and density of large downed logs, and varied across years and states. These results indicate that land managers implementing prescribed fire treatments to reduce fuel loads on public lands can reduce the impacts of fire on squirrel populations by formulating prescriptions to retain large live trees and large downed logs.

KEY WORDS Before-After-Control-Impact, fuel reduction, Idaho, point counts, ponderosa pine, prescribed fire, *Tamiasciurus hudsonicus*, Washington.

Prescribed fire is used to reduce both fuel loads and risk of future severe wildfire in coniferous forest in the western United States, although integrating objectives for managing fuel and fire risk with objectives for managing wildlife has not been addressed explicitly in design of fuel-reduction prescriptions (Lehmkuhl et al. 2007). Generalizations about the ecological effects of prescribed fire in forested ecosystems are difficult to formulate due to high variability in severity of prescribed fires due to variation in timing, frequency, intensity, weather, and prefire conditions (Tiedemann et al. 2000). Investigations on the effects of prescribed fire on wildlife communities in forests have often found variable responses by dominant plant species (Bagne et al. 2008) and by vertebrate species (Converse et al. 2006).

The red squirrel (*Tamiasciurus hudsonicus*) makes an ideal candidate for assessing effects of prescribed fire on wildlife because the species is sensitive to habitat changes that result from wildfire or logging due to its associations with large live and dead trees, downed woody debris, overstory and understory diversity, and epiphytes (Yahner 1987, Carey 1989, Holloway and Malcolm 2006). Red squirrels also perform several functions in forest ecosystems, including depredating songbird nests (Bayne et al. 1997, Sieving and Willson 1998, Willson et al. 2003), being prey for raptors and mammalian carnivores (Rusch and Reeder 1978, Steele 1998, Aubry et al. 2003, Smith et al. 2003, Carey 2005), and dispersing conifer seeds and fungal spores (Smith 1970, Maser and Maser 1988, Aubry et al. 2003). Additionally, managing habitat for squirrels and other small mammal populations is often suggested as a means of managing predators of small mammals, such as raptors (Reynolds et al. 1992, Boal et al. 2005, Carey 2005). Therefore, understanding the effects of prescribed burning on red squirrel populations is important for making inferences regarding the ecological effects of low-severity fire on forest ecosystems.

Low-severity prescribed fire can alter many important aspects of red squirrel habitat by damaging live large trees, reducing shrub cover, and reducing the volume of coarse woody debris. Prescribed fire can create or destroy large snags used as nest sites for squirrels and a variety of other cavity-nesting species (Saab et al. 2006, Bagne et al. 2008). Fire destroys seed sources and den sites, as well as ground cover used as shelter from predators (Fisher and Wilkinson 2005). Fisher et al. (2005) demonstrated that squirrels may move into suboptimal habitat (in this case, deciduous forest) in burned areas where conifer patches are not available, and Roppe and Hein (1978) found that red squirrels were entirely excluded from forests burned by wildfire. However, treatments that reduce stand densities and ground fuels as part of dry forest restoration, such as prescribed fire in combination with thinning, may increase long-term food resources for red squirrels. Nine years after thinning and prescribed fire, cone production of ponderosa pine (*Pinus ponderosa*) was nearly 8 times greater in treated versus untreated areas in western Montana, USA (Peters and Sala 2008).

In 2002, we implemented a large-scale Before-After-Control-Impact study (Green 1979, Stewart-Oaten et al. 1986) to experimentally quantify the effects of prescribed fire on wildlife, including red squirrels and their habitat in ponderosa pine–dominated ecosystems (Saab et al. 2006). We hypothesized that red squirrel densities would decline following prescribed fire due to the effects of increased opening of the tree canopy (lost foliage, decline in the live stem density) and reduced ground cover (shrubs and large

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logs). Alternatively, without loss of large trees, these treatments may have little or no effect on red squirrel populations.

STUDY AREA

We selected 10 study units ranging from 200 ha to 400 ha in 2 national forests in the Pacific Northwestern United States: the Payette National Forest in Idaho (4 study units), and the Okanogan–Wenatchee National Forest in Washington (6 study units). Overstory vegetation on all units was dominated by ponderosa pine. In both locations, the understory was comprised of shrub species, including snowberry (*Symphoricarpos albus*), spirea (*Spirea* spp.), serviceberry (*Amelanchier alnifolia*), and chokecherry (*Prunus* spp.), and the grass species bluebunch wheatgrass (*Pseudoroegnaria spicata*) and Idaho fescue (*Festuca idahoensis*; Saab et al. 2006).

METHODS

We chose study sites in Washington and Idaho from a pool of units that were scheduled for imminent operational prescribed burns by the United States Forest Service. We chose study sites based on size, accessible terrain (e.g., not too steep and rocky for safe field work), and relatively similar vegetation composition and pattern that was representative of dry forest conditions in the area. We burned 5 sites, 3 selected at random in Washington and 2 selected at random in Idaho.

We implemented prescribed fire treatments in Washington during spring of 2004 on 2 units and burned a third unit in spring of 2005. In Idaho, we burned one treatment unit in spring of 2004 and one in spring of 2006. We designed fires to reduce the number of small-diameter live stems (<15.4-cm dbh); reduce existing fuel loads, including surface and ladder fuels; and create small gaps in the upper tree canopy, yet retain large pine trees and snags (>23-cm dbh; M. Dunn, United States Forest Service, unpublished report; K. Busse and M. Trebon, United States Forest Service, unpublished report). Silvicultural objectives were to maintain a vigorous stand of fire-tolerant Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine >13-cm diameter at breast height at a typical stocking of 250–500 trees/ha, with special emphasis on retention and growth of large-diameter (>45-cm dbh) pine. We would accomplish that by reducing overall stocking of understory trees <13-cm diameter at breast height, particularly Douglas-firs with dwarf mistletoe infection or understory trees growing in clusters near canopies of vigorous mature trees. We desired open patches of <1 ha that occupied <5% of the burned area, created by locally intense fire effects.

Saab et al. (2006) documented effects of the treatments as an increase (+29%) in large snag (>23 cm) numbers, a decline in downed woody material (−59%), a decline in shrubs of all sizes (−31%), and an increase in large live tree numbers (+0.57%).

We established 10–20 100-m-radius point-count stations in each of the 10 study units, 70 point-count stations in Idaho and 120 in Washington. We located point-count stations 250 m apart and 250 m from the edge of the study unit. We visited stations in Idaho twice yearly and stations in Washington 3 times/year between 22 May and 3 July (2003–2007 in Idaho and 2002–2006 in Washington), for 360 surveys a year in Washington and 140 surveys a year in Idaho. Sample years bracketed prescribed burning with 2–4 years of preburn data and ≥2 years of postburn data. We began point counts just after dawn and completed them within 5 hours. At each point, observers recorded the number of red squirrels detected by sight or call during a 5-minute observation period and the estimated distance from the observer to each squirrel as 0–10 m, >10–25 m, >25–50 m, >50–75 m, >75–100 m, or >100 m (Bird and Burns Network 2003).

We measured vegetation in Washington and Idaho before and after prescribed fire on treated units, and we measured control units once at all locations. We sampled vegetation at each point-count station within 2 20 × 100-m perpendicular rectangular plots that crossed at the center of the station. Tree and snag measurements followed methods outlined by Bate et al. (1999). We counted standing dead stems (snags) ≥23-cm diameter at breast height within 10 m of the center line of rectangular plots, and standing live stems (large trees) ≥23-cm diameter at breast height within 3 m of each center line (Saab et al. 2006). We only counted trees in the cross-section of the plots once.

We measured downed woody material along the center line of each rectangular plot following Brown's (1974) protocol. We defined downed woody material as the "dead twigs, branches, stems, and boles of large trees and brush that have fallen and lie on or above the ground" (Brown 1974:7). For this analysis, we counted the number of large downed logs (≥23 cm at the large-end diam) along the center line of each 100-m rectangular plot.

We estimated shrub cover in 3 4-m-radius subplots. We placed 2 subplots with the center point at either end of the 100-m north–south transect, and the third was placed in the center of the crossed 100-m transects. We estimated percent cover of shrubs ≤1 m in height at 32 points with each of the subplots. We took measurements every 0.5 m in each of the 4 cardinal directions from the center point of each plot by lowering a dowel perpendicular to the meter tape and tallying the number of times the dowel touched a shrub.

We estimated density of squirrels by modeling counts as a function of covariates (Buckland et al., in press). For point-transect sampling, we calculated density in plot (k) by

$$\hat{D}_k = n_k \frac{H_k}{2\pi e_k}$$

where e_k = total effort conducted on plot k (i.e., no. of visits to a point count by no. of point counts/study unit), n_k = number of animal clusters detected on plot k, and $H_k = (1/n_k)\Sigma_{i=1}^{n_k} s_i \hat{h}_{y|z}(0 \mid \underline{z}_i)$ where s_i = number of animals in ith detected cluster on plot k, $\hat{h}_{y|z}(y \mid \underline{z}_i) = \hat{f}_{y|z}'(y \mid \underline{z}_i)$ = slope of estimated probability density function of distance y from the point for ith detected cluster on plot k, for covariates $\underline{z}_i$ and $\hat{h}_{y|z}(0|\underline{z}_i) = \hat{h}_{y|z}(y|\underline{z}_i)$ at $y = 0$. We then

Table 1. Model-selection results for top models of detection probability as a function of distance and habitat covariates. We modeled detection probability for squirrel observations on 10 study units in 2 national forests in Idaho and Washington, USA, from 2002 to 2007. We treated half of all study units with prescribed fire 2004–2006.

Model	No. parameters	ΔAIC[a]	AIC[a]
Trees and shrubs	3	0.00	2,530.78
Trees, shrubs, and yr	8	1.50	2,532.29
Trees	2	4.29	2,535.07

[a] AIC = Akaike's Information Criterion.

modeled counts as a generalized linear model (GLM) with a Poisson error distribution, a log link function, and an offset that accounted for imperfect detection [$-\log_e (H_k/2\pi e_k)$].

First, we modeled detection probability using Program Distance (Thomas et al. 2005). We used the multiple-covariate distance-sampling engine and compared candidate models that included the variables year, state (WA or ID), fire treatment (whether the study unit was a control or a treatment unit), time period (before or after treatments were implemented on the treatment units), log density, tree density, shrub cover, and snag density. We evaluated models using Akaike's Information Criterion (AIC) model-selection approach (Burnham and Anderson 2002). We estimated our detection function as a global detection function that incorporates all data from all study plots in all years.

To account for uncertainty in the detection function and, therefore, in estimates of H_k and offset, we performed a 2-stage bootstrap. First, we resampled data with replacement from point counts within study units to generate 1,000 bootstrapped resamples. Resample data sets contained data from 20 point-count stations for 9 study units, and 10 point-count stations for one study unit. If a point count was selected in the resample, then all of the data from all visits to that point count were selected; therefore, any correlation in counts in different years for a given point is preserved in the resamples, and inference based on the bootstrapped samples does not assume independence. For each bootstrapped data set, we re-estimated the H_k and the offset for each study unit in each year.

Second, for each bootstrapped sample, we modeled squirrel counts/study unit/year using the GLM function inside the package stats (Buckland et al., in press; R Development Core Team 2007). Candidate models of red squirrel density included effects of state, year, fire treatment, time period, snag density, tree density, log density, and shrub cover both separately and in combination, and a null model including the offset only for 40 models. To assess effects of prescribed burning, we modeled density as a function of fire treatment, time period, and fire treatment × time period interaction. We also included a model that accounted for potential differences in treatment effects by state, by modeling density as a function of state, treatment, time period, and all 2- and 3-factor interactions.

We estimated the effect of habitat covariates in the best models by calculating predicted densities for different levels of a particular variable, while holding the other variables constant and determining what value corresponded to a doubling of predicted squirrel densities. This process is equivalent to calculating $\exp(\beta_1)$ where β_1 is a parameter estimate for covariate one, and what value of z is necessary to result in $\exp(z\times\beta_1) = 2\times\exp(\beta_1)$.

Table 2. Top regression models of squirrel densities on 10 study units in 2 national forests in Idaho and Washington, USA, from 2002 to 2007. We treated half of all study units with prescribed fire 2004–2006. We selected top models from 1,000 bootstrap resamples, and reported mean Akaike's Information Criterion (AIC) value from these 1,000 data sets along with the number of parameters in the model (K), ΔAIC, and the percentage of times (out of 1,000) the model was selected as the best model for the bootstrapped data sets.

Model	Mean AIC	K	ΔAIC	% best model
State, yr, shrubs, logs, and trees	1,817.64	10	0.00	94.60
State, yr, shrubs, and logs	1,819.69	8	2.05	5.40
Yr, trees, shrubs, and logs	1,834.02	9	16.38	0.00

We evaluated all candidate models for each of the 1,000 bootstrap resamples by calculating an AIC value for each model, and tallying the number of times each model had the lowest AIC value across the 1,000 resamples. We also calculated an average AIC value for each model to calculate overall differences (ΔAIC) in AIC between models. If our data provided evidence for an effect of prescribed fire on squirrel density, a model containing the type × treatment (or state × type × treatment) interaction would have been selected as the best model or would have had an AIC value <2 points away from top models.

RESULTS

We detected 928 squirrels during the study period. Most of these were single observations ($n = 901$) with 12 clusters of 2 squirrels and 1 cluster of 3 squirrels detected. Mean cluster size was 1.02 ± 0.01 standard error. The probability of detection of a squirrel decreased with increasing tree density and shrub cover (Table 1).

We found no evidence of an effect of prescribed fire on red squirrel densities. We estimated the difference in squirrel density on the treatment sites before and after fire was implemented as −0.32 squirrels/ha (95% CI = −0.493–0.147). Control sites were unburned, and we estimated the difference in squirrel density on control sites prior to fire treatments on treated sites and after treatments were implemented at −0.17 squirrels/ha (95% CI = −0.359–0.019). Squirrel density increased with tree density, shrub cover, and log density, and varied by state and year, as predicted by the best models (Tables 2, 3). Overall estimates of squirrel density were higher in Washington than Idaho (Table 3; Fig. 1). The parameter estimate for Washington versus Idaho was >0 (1.033, 95% CI = 0.440–1.429; Table 3), and confidence limits for density estimates did not overlap for Idaho and Washington in any year (Fig. 1). Predicted squirrel density at 70 trees/ha and average shrub cover and log density were 0.27 squirrels/ha (95% CI = 0.21–0.34) in Idaho and 1.04 squirrels/ha (95% CI = 0.80–1.35) in Washington (approx. 3.85× higher). Estimates of squirrel density were highest in Washington in the year 2002 and averaged 1.27 squirrels/ha (95% CI = 1.09–1.72)

Table 3. Parameter estimates for best model of squirrel counts on 10 study units in 2 national forests in Idaho and Washington, USA, from 2002 to 2007. We treated half of all study units with prescribed fire 2004–2006. We estimated confidence limits (LCL = lower 95% CL, UCL = upper 95% CL) from 1,000 bootstrapped data sets.

Parameter	LCL	$\bar{x}$	UCL
Intercept	−11.815	−10.005	−9.558
State (WA vs. ID)	0.440	1.033	1.429
Yr (2002 as reference)			
2003	−0.895	−0.465	0.522
2004	−3.107	−2.336	−0.835
2005	−1.867	−1.418	−0.447
2006	−1.085	−0.857	0.217
2007	−3.902	−1.263	−0.129
Trees	0.004	0.012	0.014
Shrubs	0.072	0.089	0.123
Logs	0.000	0.004	0.012

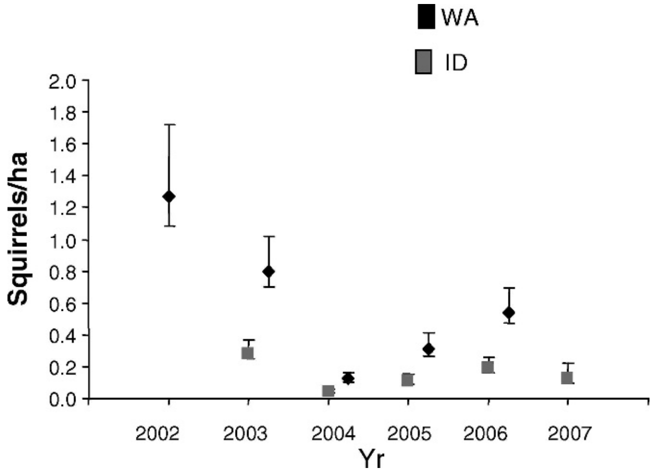

Figure 1. Estimates of squirrel densities/ha for each study unit (one study unit = 250–400 ha) in 2 national forests in Idaho and Washington, USA, from 2002 to 2007. We treated 5 of 10 study units with prescribed fire 2004–2006. Estimates are predicted values and 95% confidence limits (error bars) from Poisson regression models containing effects of state, year, tree density, shrub cover, and log density. We estimated densities at mean values of tree density, shrub cover, and log density for each state and year.

and were lowest in Idaho in 2004 (0.04 squirrels/ha, 95% CI = 0.04–0.06). An increase in tree density by 60 trees/ha roughly doubled the predicted squirrel densities. For example, in Washington predicted squirrel densities increased from 0.51 squirrels/ha (95% CI = 0.36–0.73) at 10 trees/ha to 1.04 squirrels/ha (95% CI = 0.80–1.35) at 70 trees/ha. An increase of 8% shrub cover corresponded to a doubling of predicted squirrel density. Density of logs had the least effect on densities of squirrel; an increase of 175 logs/ha was necessary to result in a doubling of predicted squirrel densities.

DISCUSSION

Underburning with prescribed fire had no detectable short-term effect on red squirrel density on our study sites in ponderosa-pine–dominated ecosystems in the northwestern United States. Despite documented reductions in shrub cover and downed woody debris after prescribed fire (Saab et al. 2006), we found no evidence of an effect of prescribed fire on red squirrel density, likely due to the retention of large live trees following the prescribed fire treatments. These results are similar to Kirkpatrick and Mosby (1981), who found no impacts of low-severity prescribed fire on tree squirrels. In contrast, in a subalpine fir forest in central Washington, Douglas' squirrel (*Tamiasciurus douglasii*) populations declined after a prescribed fire that resulted in a reduction of basal area of live trees and overstory canopy cover (Hanson 1978, Tiedemann and Woodard 2002). Low-severity prescribed fire that remains on the ground and does not become a crown fire will likely have little impact on red squirrels (Kirkpatrick and Mosby 1981, Koprowski et al. 2006). Squirrels can escape into the canopy to avoid surface fires, and surface fires will not kill juveniles that are still in the natal nest (Koprowski et al. 2006).

Although we did not detect any large changes in squirrel density after fire, shifts in the age structure, body mass, or fitness of the postfire population may have occurred. Previous studies have noted suboptimal habitat may be occupied by immature or dispersing individuals (VanHorne 1983, Sullivan and Moses 1986). Squirrel density possibly remained fairly constant after prescribed fire due to an influx of juvenile squirrels during the year between burning and 1 year after burning. Adult red squirrels are territorial and will actively defend their territories, thus potentially driving younger animals into sub-prime habitat (Smith 1968, Kemp and Keith 1970, Koford 1982). Rusch and Reeder (1978) noted that adult Alberta red squirrels comprised a higher percentage of the population in spruce (*Picea mariana* and *P. alba*) habitat versus less preferred jack pine (*Pinus banksiana*) or aspen (*Populus tremuloides*). Several studies have noted a spring shuffle, whereby squirrels redistribute and mature individuals obtain prime territories (Rusch and Reeder 1978, Wheatley et al. 2002). Additionally, body mass rather than density may also change as a function of habitat and act as an indicator of individual fitness and habitat quality (Wheatley et al. 2002, Herbers and Klenner 2007).

Longer term studies are necessary to determine how squirrel densities might change with recovery of forest vegetation after fire. Herbers and Klenner (2007) noted that red squirrel densities did not respond to logging treatments until 2–4 years posttreatment. Wheatley et al. (2002) observed a 50% reduction in red squirrel densities in spruce (*Picea glauca*) habitat after 1 year of cone failure. Red squirrel abundance is closely tied to cone crops and conifer seed abundance (Kemp and Keith 1970, Smith 1970), which are affected by time since treatment and vary widely over time. Peters and Sala (2008) found cone production of ponderosa pine in western Montana to be nearly 8× greater in thinned and burned stands than in untreated stands 8 years after treatment. Heavy ponderosa pine cone crops occur at 2–8-year intervals across its range, depending on the location (Oliver and Ryker 1990). Lag responses in squirrels and fluctuation in food abundance over time may affect squirrel densities, thus indicating the need for long-term monitoring.

Results of our prescribed fire study do not reflect potential effects of more intense prescribed fires that result in significant canopy mortality or of stand-replacement wildfire on squirrel densities. Koprowski et al. (2006) reported a 35% loss of radiocollared Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) over a 14-day period following a wildfire that produced areas of intensive crown fire. Red squirrel density did not change in the short term in response to the low-severity prescribed fire in our study, but responses elsewhere will be dependent on local vegetation conditions, the timing, size, and severity of burns, the length of time since burn, and landscape-level factors such as the availability of source habitat and the predator community.

MANAGEMENT IMPLICATIONS

Land managers implementing low-severity prescribed fire treatments should not expect short-term changes in squirrel densities on treated areas. Typical fuel-reduction objectives to reduce fine fuels and ladder fuels (small understory trees) likely would not affect red squirrels. Treatments that aim to retain large trees and downed logs could maintain squirrel populations in the treated area. Large downed logs typically are not targeted for reduction because they have little influence on wildfire behavior (Agee 1993); however, some logs are destroyed depending on local burn conditions (Saab et al. 2006). The objective of reducing understory stocking and competition with large trees likely will enhance squirrel habitat by producing large vigorous trees with good cone crops (Peters and Sala 2008) and allowing for the development of large snags suitable for cavity development (Van Pelt 2008). Managers should expect increasingly short- and long-term detrimental effects of burning on red squirrels with increasing fire intensity.

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